

Phytogeography of *Pelargonium*

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ABSTRACT

The vast majority of the approximately 200 species of *Pelargonium* occurs in Africa. About 80 per cent of the species are endemic to the winter rainfall region of the Cape Province, and the centre of distribution lies in the south-western Cape.

The distribution of the individual sections are discussed with the aid of distribution maps. The centre of distribution of most sections is in the south-western Cape, but a few sections are centred in the eastern and western Cape. Several sections are represented by a few species in the summer rainfall region of southern Africa.

As no fossils of *Pelargonium* are known, deductions about the origin of the genus can only be based on the present distribution of species, according to which arguments in favour of both a northern and a southern origin can be supported.

RÉSUMÉ

PHYTOGÉOGRAPHIE DES PELARGONIUM

La vaste majorité d'approximativement 200 espèces de *Pelargonium* se trouve en Afrique. Environ 80% de ces espèces sont endémiques à la région à pluies d'hiver de la province du Cap et le centre de distribution est situé dans le Sud-Ouest du Cap.

La distribution des sections individuelles est discutée à l'aide de cartes de distribution. Le centre de distribution de la plupart des sections est dans le Sud-Ouest du Cap, mais quelques sections sont centrées dans l'Est et l'Ouest du Cap. Plusieurs sections sont représentées par quelques espèces dans la région à pluies d'été de l'Afrique australe.

Comme aucun *Pelargonium* fossile n'est connu, les déductions sur l'origine du genre peuvent seulement se baser sur la distribution actuelle des espèces, qui permet d'avancer des arguments en faveur d'une origine à la fois australe et nordique.

INTRODUCTION

The genus *Pelargonium* was last revised by Knuth (1912) who recognized some 227 species which were accommodated in 15 sections. Knuth completely omitted *P. cotyledonis* (L.) L'Hérit. which we here place in a sixteenth and monotypic section, *Isopetalum* Sweet. Since 1912 a number of additional species have been described, but our revisionary work on the genus indicates that a number of species recognized by Knuth should be placed in synonymy (Van der Walt, 1977; Van der Walt & Vorster, 1981). On the other hand, a number of still undescribed species are known to us.

Goldblatt (1978) mentioned the Geraniaceae as one of the characteristic families of the Cape Floristic Region. This statement is based on the fact that the vast majority of *Pelargonium* species occur in the south-western Cape Province. Outside South Africa, the genus is represented by 18 species in the rest of Africa, eight in Australasia (Carolin, 1961; Swinbourne, 1970), two on Madagascar, two in Asia Minor and one each on the island of St Helena and Tristan de Cunha (Fig. 1).

The aim of the present paper is to present a global picture of the natural distribution of the genus and its sections. The survey is based on an intensive study of about 160 species occurring within the Flora of Southern Africa (FSA) region, whereas the distribution data for non-South African species were taken from herbarium specimens and literature.

DISTRIBUTION OF THE GENUS

The genus has a wide distribution practically throughout the FSA area (Fig. 2). However, by far the highest concentration of species is found in the south-western Cape Province, an area receiving winter rain. The one degree squares including the towns of Worcester and Cape Town have the highest concentration of species (Fig. 3.1). Fairly high concentrations of species are also found along the west coast extending to near the Orange River, and eastwards to the Cape/Transkei border. These areas receive rain either exclusively in winter or throughout the year.

The distribution of the genus coincides largely with that of Fynbos, but it can also be found in other vegetation types, such as grassland. Furthermore, although a high percentage of the species occurs in mountainous terrain on sandstone substrates, the genus is by no means confined to sandstone, and even geophytic representatives of the sections *Hoarea* (Sweet) DC. and *Seymouria* (Sweet) Harv. are sometimes found on heavy soils. On the whole, one of the most important factors determining the distribution of the genus probably is mild climatic conditions during the growing season. Generally the genus is absent in areas where the growing season is very hot. Over most of the distribution area, the plants are not subjected to temperatures far below freezing point during the growing season. In those parts of the distribution area where the summers become very hot or the winters very cold, the plants tend to die back and become dormant for the duration of the unfavourable season.

Although there is a dearth of information concerning the environmental conditions exper-

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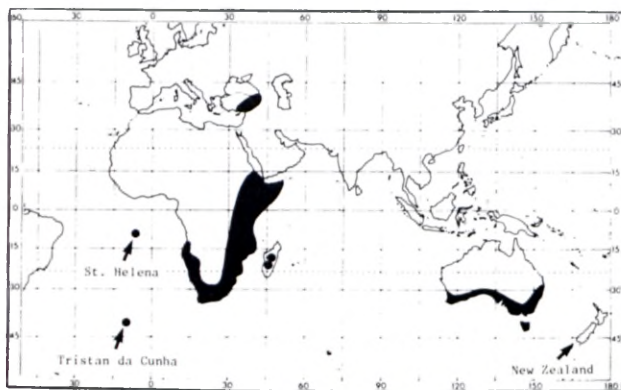


FIG. 1.—World distribution of the genus *Pelargonium*.

enced by the geographically more remote species, it is noteworthy that both the species in Asia Minor and Australasia occur between 30 and 40 degrees of latitude. The Australian species occur under climatic conditions not dissimilar to those reigning in the south-western Cape Province, and it is not unreasonable to accept that the basic environmental requirements of the genus are more or less similar for the majority of species. Apparently paradoxical is the occurrence of the genus in tropical east Africa, but it should be pointed out that these species are mostly associated with cool highlands which constitute a summer rainfall growing season climatically resembling the winter rainfall growing season experienced elsewhere.

DISTRIBUTION OF THE SECTIONS

The section *Pelargonium* is considered to be the most primitive section of the genus on account of its rather woody, much-branched, shrubby habit, simple leaves, and five-petalled flowers with seven fertile stamens. The 24 species occur in the south-western, southern and eastern Cape, extending northwards along the eastern escarpment (Fig. 3.2) to the eastern highlands of Zimbabwe. The two highest concentrations of species, in the south-western and southern Cape, fall entirely in the winter rainfall region. Many of them, however, do not occur in close association with Fynbos, but rather favour primitive, moist, shaded habitats, often in association with forest precursors. The species in the eastern Cape receive rain in winter as well as in summer, whereas those in the Transkei occur in a predominantly summer rainfall region. *P. graveolens* L'Hérit. extends through the summer rainfall area, from the eastern Cape to the eastern highlands of Zimbabwe (Müller, 1963), often in association with relic patches of high mountain Fynbos.

The section *Eumorpha* (Eckl. & Zeyh.) Harv. consists of subshrubs with only the bases of the stems woody. It is also considered to be a primitive section, because of its simple leaves and five-petalled flowers with mostly seven (rarely six) fertile stamens. Five of the eight species occur in the winter rainfall area with the highest concentration of species in the extreme south-western Cape Province. Of the species occurring outside the winter rainfall region, *P. transvaalense* Knuth is confined to a small

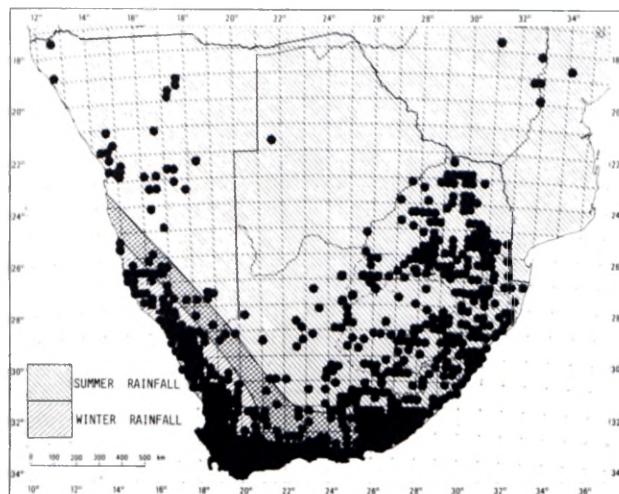


FIG. 2.—Distribution of the genus *Pelargonium* in the Flora of Southern Africa region.

area in the eastern Transvaal, whereas *P. alchemiloides* (L.) L'Hérit. occurs throughout the winter rainfall region and extends north-eastwards through the summer rainfall region (Fig. 3.3), possibly as far as Zimbabwe. In tropical east Africa (Kokwaro, 1971), the section is represented by two species.

The section *Ciconium* (Sweet) Harv. is also considered to be one of the primitive sections on account of the simple leaves and the almost regular five-petalled flowers. It does, however, exhibit certain advanced characters e.g. the herbaceous to semi-succulent stems of the subshrubs/shrubs, and in some species a reduced number of five fertile stamens. The sectional centre of distribution lies in the eastern Cape Province where three of the four species are concentrated, two of them endemic to that area. The third species, *P. zonale* (L.) L'Hérit., extends westwards far into the winter rainfall region, and a fourth species, *P. acraeum* R. A. Dyer, is endemic to the escarpment of Natal and the eastern Transvaal (Fig. 3.4). The eastern Cape populations get rain throughout the year, the Natal and Transvaal populations of *P. acraeum* summer rains, and *P. zonale* experiences winter rains where it intrudes into the winter rainfall area. The impression was gained that this is essentially not a winter rainfall section. *P. zonale*, the only species which occurs in both the summer and winter rainfall regions, is not plentiful in the winter rainfall region compared to its abundance further east where it experiences summer rain, and the species outside the purely winter rainfall area are usually not associated with Fynbos vegetation.

Although the section *Peristera* DC. consists of annuals or short-lived perennial herbs, many species exhibit primitive characters such as simple leaves and rather regular five-petalled flowers with seven fertile stamens. Advanced characters such as a reduction of the number of petals and fertile stamens, are found in some representatives. In its present circumscription it includes a group of thirteen species in South Africa, extending northwards to the escarpment between Zimbabwe and Mozambique. It also includes one species in east

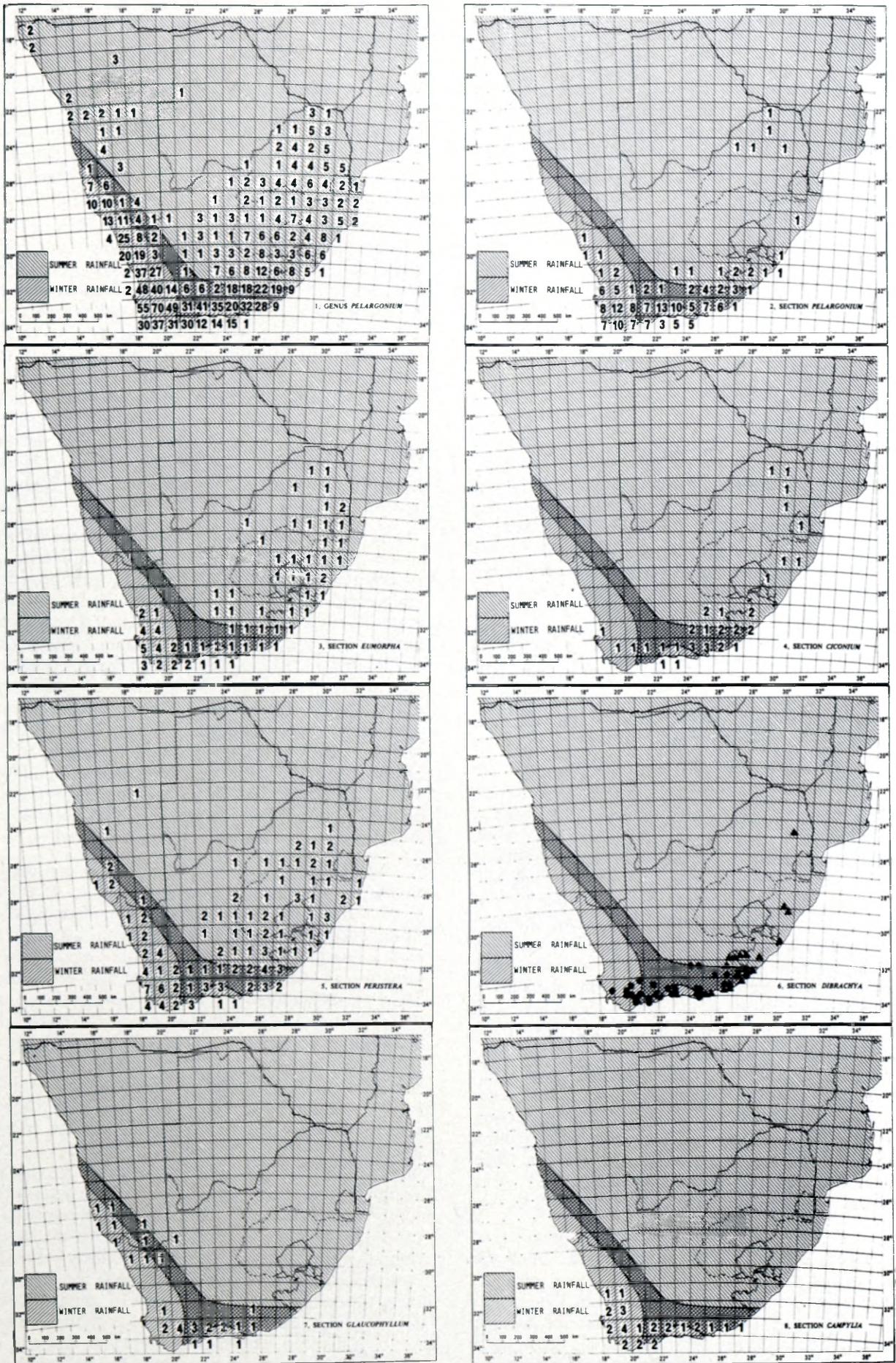


FIG. 3.—Distribution and concentration in the Flora of Southern Africa region of species of: 1, genus *Pelargonium*; 2, section *Pelargonium*; 3, section *Eumorpha*; 4, section *Ciconium*; 5, section *Peristera*; 6, section *Dibrachya* — ▲ *P. lateripes*, ● *P. peltatum*; 7, section *Glaucophyllum*; 8, section *Campylia*.

Africa, one or possibly two in Madagascar, one on the island of Tristan da Cunha and eight species in Australasia. It is possible that some of the non-South African species should be excluded from this section. The individual South African species tend to have surprisingly large distribution ranges, with at least half of them occurring in both the summer and winter rainfall areas. In South Africa the highest concentration of species occurs in the south-western Cape Province (Fig. 3.5). However, it is evident that the distribution of many species is not determined by either winter or summer rainfall. It is significant that several of the South African species have developed an annual habit to enable them to survive the dry season. As far as habitat preference is concerned, it is noteworthy that the non-South African species occur under conditions similar to those of the South African species.

The Section *Dibrachya* (Sweet) Harv. shows several advanced characters, such as a scrambling habit with relatively thin stems, somewhat succulent leaves, irregular flowers and often a reduced complement of fertile stamens. Primitive characters such as simple leaves and seven fertile stamens may indicate a relationship with the primitive section *Eumorpha*; in fact, a natural hybrid between these two sections has been reported. This section consists of two groups of populations, which may or may not be conspecific. The distribution of *P. peltatum* (L.) L'Hérit is very well correlated with the winter rainfall region of the south-western, southern and eastern Cape Province, although part of its range receives rain in summer as well. *P. lateripes* L'Hérit. occurs in the eastern Cape where its range overlaps with that of *P. peltatum*, and it is also found in the summer rainfall region of the Transkei, Natal and the eastern Transvaal (Fig. 3.6).

The section *Glaucophyllum* Harv. is advanced in respect of its herbaceous to semi-succulent stems, the unifoliolate or trifoliolate leaves, and reduced number of five fertile stamens in some species. However, the general floral structure (five petals) shows a link with the section *Pelargonium*, and this relationship is supported by the occurrence of natural hybrids between the two sections. This section of five species comprises a natural group of four species which occurs in low, dry shrubland from the eastern to the south-western Cape, within the winter rainfall region. The fifth species, *P. spinosum* Willd., is provisionally included in this section, but morphologically and phytogeographically it differs to such an extent from the mainstream of the section that it may be prudent to exclude it from this section altogether. It occurs in the north-western Cape Province and southern South West Africa on rocky outcrops under severely dry conditions (Fig. 3.7).

The section *Campylia* (Sweet) DC. consists of herbaceous subshrubs with simple leaves. There are four or five petals per flower, and the number of fertile stamens varies from five to seven. The nectar tube of the flower is usually shorter than the pedicel, in some species very short indeed. There is a remarkable resemblance between the flowers of certain species of the sections *Campylia* and *Pelargonium*, which may be indicative of a

relationship between them. The distribution of the seven species of this section is well correlated with the winter rainfall region, with the highest concentration of species in the south-western Cape Province (Fig. 3.8). These plants have unswollen subterranean parts of considerable extent, often much more extensive than the exposed parts, which enable them to survive the hot and dry summers when the plants are dormant. This section is typically associated with low-lying, sandy flats.

The section *Otidia* (Lindl. ex Sweet) DC. consists of succulent subshrubs or shrubs with relatively thick branches. The rather regular flowers have five petals and five fertile stamens each. This section may be related to the monotypic section *Isopetalum* (Sweet) DC., which also has succulent stems and almost actinomorphic flowers. The seven species of the section *Otidia* occur within the winter rainfall region, with one species extending into the summer rainfall parts of the Cape Province. The largest concentration of species occurs along the western Cape coast (Fig. 4.1). These plants are well adapted to survive dry summers by virtue of their succulence and deciduous habit.

The section *Isopetalum* (Sweet) DC. consists of a single species, *P. cotyledonis* (L.) L'Hérit., a succulent subshrub with relatively thick branches and simple leaves. The flowers are regular with five petals, five or six fertile stamens, and a very short nectar tube. Its present very isolated geographical location on the island of St Helena (Fig. 1) does not appear to have great phytogeographical significance, but probably signifies that *P. cotyledonis* became isolated from the rest of the genus at an early stage and proceeded to adapt itself morphologically to the particular set of conditions reigning in its limited area of distribution, while at the same time retaining certain primitive characters which does not place it at a disadvantage where survival is concerned.

The section *Cortusina* (DC.) Harv. consists of subshrubs or shrubs, often with thick succulent branches, and simple leaves. The five-petalled flowers are rather regular, and there are six or seven fertile stamens. Similarities exist between the floral structure of the sections *Cortusina* and *Polyactium* DC., possibly indicating a relationship between the two sections. This affinity is supported by the presence of subterranean tubers in some species of *Cortusina*. The nine species of this section occur in southern S.W.A./Namibia, the western, south-western and eastern Cape Province, and thence northwards through the Orange Free State to the Transvaal (Fig. 4.2). Typically, the plants occur under rather dry conditions, which they survive by virtue of the succulence of the exposed and/or subterranean parts. The distribution of the section is to a considerable extent correlated with winter rainfall, although the centre of distribution lies in the eastern Cape in an area which in part receives rain throughout the year, and in part in summer only. Most species are rather restricted in their distribution, but there are two exceptions, namely *P. sidifolium* (Thunb.) Knuth and *P. odoratissimum* (L.) L'Hérit., which extend into the summer rainfall region.

The section *Polyactium* DC. consists of geophytes with relatively large subterranean tubers. The leaves are simple to palmately or pinnately compound, radical and often heteroblastic. The flowers are rather regular with five petals and six or seven (exceptionally five) fertile stamens. Twelve of the thirteen species of this section are concentrated in a 200 km wide strip along the coast. To a large extent the distribution of these species are well correlated with the winter rainfall region. Two areas of concentration can be discerned, namely a major concentration in the south-western Cape Province and a secondary concentration in the eastern Cape. The abundance of species in the eastern Cape centre of distribution should be ascribed to the presence of an endemic eastern group, namely the *P. schizopetalum* Sweet — *P. caffrum* (Eckl. & Zeyh.) Harv. — *P. bowkeri* Harv. group. *P. luridum* (Andr.) Sweet has a very wide distribution and apart from a few scattered records from the southern Cape where it rains throughout the year, this is essentially a summer rainfall species (Fig. 4.3).

The section *Ligularia* (Eckl. & Zeyh.) Harv. comprises woody or herbaceous subshrubs with simple to compound leaves. The flowers have four to five petals each, and five or seven fertile stamens. The floral structure and vegetative characters suggest a relationship with the sections *Myrrhidium* DC. and *Jenkinsonia* (Sweet) DC. This section of about 27 species has a wide distribution throughout the FSA region (Fig. 4.4). Two definite areas of concentration can be discerned, namely in the south-western and western Cape Province where most species occur under winter rainfall conditions, and another in the eastern Cape Province under predominantly summer rainfall conditions.

The section *Jenkinsonia* (Sweet) DC. consists of woody, herbaceous or succulent subshrubs/shrubs with simple leaves. The inflorescences are borne on ordinary branches and consist of pseudo-umbels of one to five flowers each. The nectar tube of the flower is much longer than the pedicel. Each flower has four or five petals and seven fertile stamens. This section is most probably related to the sections *Myrrhidium* and *Ligularia*. The distribution area of the three species of the section *Jenkinsonia* is well correlated with the winter rainfall region of the Cape Province, although the eastern part of the range receives rain in summer as well. The species are usually found under rather dry conditions, where they form a component of low, dry shrubland (Fig. 4.5).

The section *Myrrhidium* DC. exhibits many advanced characters, namely herbaceous, trailing stems, compound leaves and a reduced number of four petals and five fertile stamens in several species. It shows a relationship to the sections *Ligularia* and *Jenkinsonia*. This section is also concentrated in the winter rainfall region where all five the presently recognized species occur, with the highest concentration in the Bredasdorp area. One species extends northwards along the eastern escarpment to the summer rainfall area through Natal and Transvaal (Fig. 4.6).

The sections *Hoarea* (Sweet) DC. and *Seymouria* (Sweet) Harv. are considered to be the most advanced sections because of their geophytic habit and the reduction of floral parts. In the section *Seymouria*, the number of petals is reduced to two, and in some species of the section *Hoarea* the number of fertile stamens is reduced to three or even two. These reductions result in pronouncedly zygomorphic flowers. Although the section *Hoarea* is the largest section in the genus, it has a rather limited distribution, coinciding almost entirely with the winter rainfall area of the south-western and western Cape Province, with only a few species present in the area which receives summer as well as winter rain. By far the highest concentration of species of the section *Hoarea* is known from the extreme south-western Cape (Fig. 4.7).

The section *Seymouria* is found in the south-western and western Cape Province under low winter rainfall conditions with the largest concentration of species in the south-west, but somewhat unexpectedly one population occurs near Knysna in the southern Cape under rather high rainfall conditions (Fig. 4.8). The plants of these sections are well equipped to survive the long, dry summer season by means of their underground tuberous parts.

DISCUSSION

The centre of distribution of most sections of *Pelargonium* is in the south-western Cape, but a few sections are centred in the eastern and western Cape. The following sections are clearly centred in the south-western Cape: *Eumorpha*, *Peristera*, *Campylia*, *Polyactium*, *Hoarea* and *Seymouria*. The sections *Ciconium* and *Cortusina* have their centres of distribution in the eastern Cape, whereas the sections *Otidia* and *Jenkinsonia* are centred in the western Cape. The sections *Pelargonium* and *Glaucophyllum* have centres of distribution in the south-western Cape as well as in the southern Cape, and *Ligularia* in the south-western and in the eastern Cape.

Several sections, though occurring mainly in the winter rainfall region, have one or more species extending through the summer rainfall region, e.g. the sections *Pelargonium*, *Eumorpha*, *Ligularia*, *Polyactium* and *Myrrhidium*. These species generally have a very wide distribution in the summer rainfall region. It is noteworthy that the section *Eumorpha*, which is considered to be one of the most primitive sections, is also represented in tropical east Africa, whereas the sections *Hoarea* and *Seymouria* which are considered to be the most advanced sections of the genus, are restricted to the winter rainfall region of the Cape Province.

As no fossil material of *Pelargonium* is known, deductions about the centre of origin of the genus can only be made on the present distribution of the species. The origin of the Cape Flora has always been a matter of controversy amongst botanists. There are followers of a temperate southern origin, and followers of a tropical origin. Willis (1922) theorized that the centre of variation of a genus

coincides with the area of origin, and the very pronounced centre of variation of *Pelargonium* in the south-western Cape, tempts one to accept this as being also the centre of origin. White (1971) warned against the danger of adhering to such views, and pointed out that there had been so much climatic and physiographic change since the origin of many genera of flowering plants, that the phytochoria to which they belong would have been destroyed if they had not migrated, often for considerable distances. Support for a tropical origin of *Pelargonium* could be found in the fact that the presumed primitive sections are represented in tropical areas.

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